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# Some General Aspects of Interhemispheric Integration*

**by ROGER W. SPERRY**

California Institute of Technology, Pasadena, California

THE TOPIC of this session leads us directly, of course, to the corpus callosum. Between 1900 and 1950, this structure had acquired a notable reputation for being, among all brain structures, the "largest, most useless." Many still remember Warren McCulloch's summary of the status of our knowledge, about 1940, with his jocular comment that the only demonstrated function for this structure seems to be that of aiding in the transmission of epileptic seizures from one to the other side of the body. More than 10 years later, Lashley still found ample justification to use his own facetious surmise that probably the principal function of this structure was not so much excitatory in nature as mechanical, i.e., to keep the two hemispheres from sagging.

The past ten years have changed the situation considerably. In a series of animal experiments, it has been possible to demonstrate, at last, definite and important functions for the corpus callosum. The first convincing evidence in this direction came from a series of investigations by Ronald Myers (1956, 1961), dealing with the function of the callosum in the interhemispheric transfer of visual discrimination learning in chiasma-sectioned cats. As illustrated in Figure 1, the mammal with crossed optic fibers sectioned in the chiasma retains the major part of its visual field, but stereoscopic overlap is eliminated and each eye feeds only to its homolateral hemisphere. What Myers found here, in brief, was that cats, trained with one eye masked, were unable to remember

* Chairman's informal introduction to the session on Interhemispheric Problems.

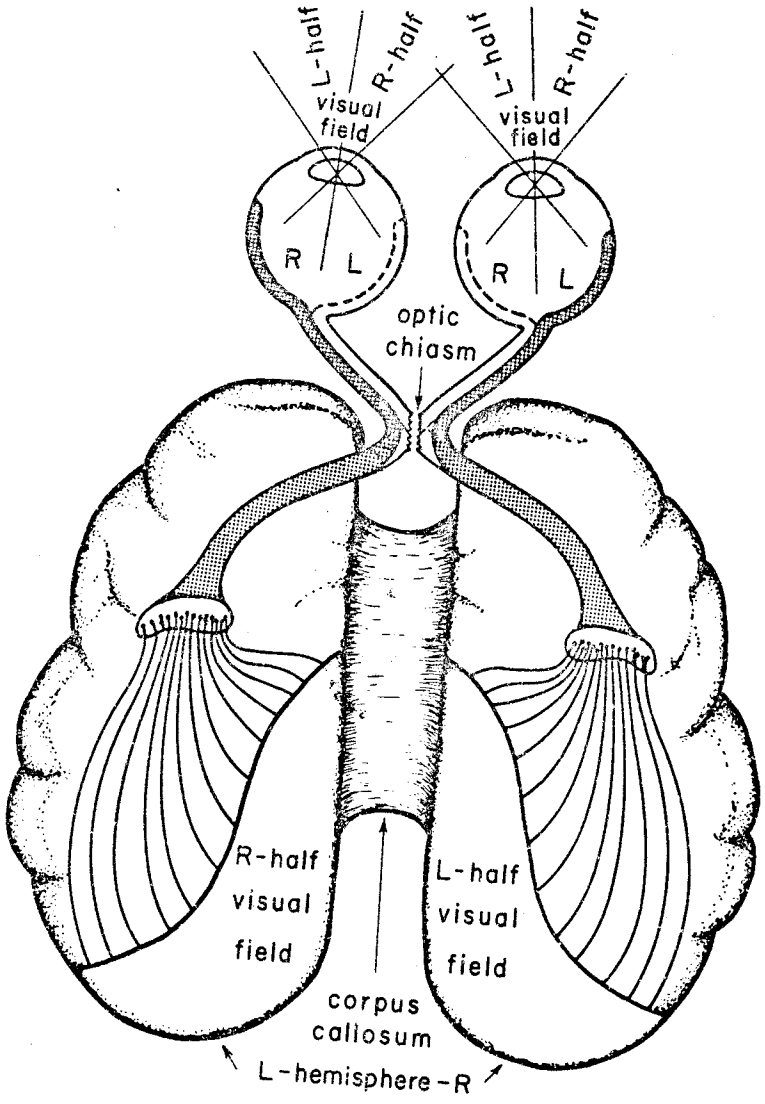
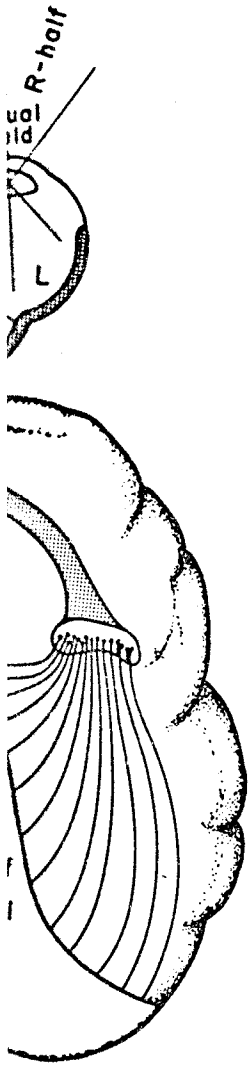



*Fig. 1.* Sketch indicating effects of midsagittal division of optic chiasma.

with the second eye what they had learned with the first eye, after both the optic chiasma and corpus callosum had been sectioned previously. In fact the second, or untrained eye, could be used to learn just the reverse of what the cat had been trained to do through the first, and

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apparently with no interference. This functional independence of the surgically separated hemispheres with respect to learning, memory, and other gnostic activity has since been amply substantiated, as will be evident in the discussion to follow.

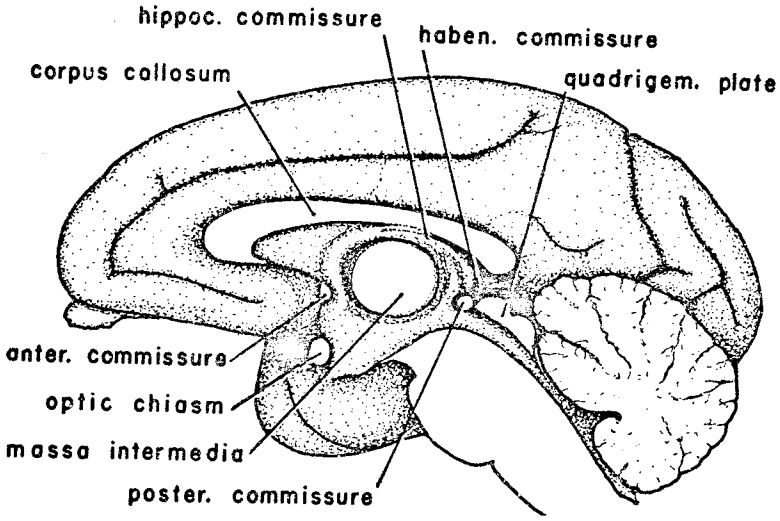



*Fig. 2.* Midsagittal aspect of monkey brain showing main structures involved in surgical bisection.

Figure 2 will recall the relations of some of the main mid-line structures involved in cross-integration in the mammalian brain. Our current mid-line surgery has been developed to the stage where we can now safely divide along with the optic chiasma, corpus callosum, and other forebrain commissures, the habenular and posterior commissures, the massa intermedia, the quadrigeminal plate, the rostral tegmentum, and the cerebellum in the monkey. This leaves undivided, at higher levels only, the remaining tegmentum and the pons. Dr. Voneida (1961) has succeeded in bringing cats through bisections that extend through the tegmentum to about midway through the pons. Cats with this extensive split, including the tegmentum, show marked cerebellar-like unsteadiness and an unexplained visual impairment immediately following the surgery. However, the animals recover and, in a month or so, their general behavior is much like normal to casual observation, excepting for some residual ataxia and visual weakness. Specific testing for perceptual, learning, memory, and emotional characteristics in these tegmental splits has only been started.

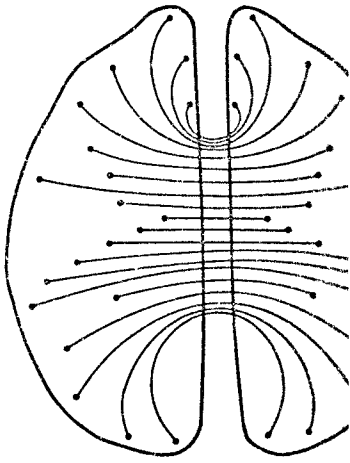
In any case, it is evident that this kind of mid-line surgery makes possible functional testing of the various brain commissures, as well as the anatomical and electrical tracing of their connections. One can section or leave intact specific segments of the callosum, or one or another of the lesser commissures in different combinations. The feasibility of thus splitting the brain into two rather independent halves also opens numerous analytic potentialities for attacking other physiological and behavioral problems. This becomes a rather lengthy subject in itself (Sperry, 1961) that we can hardly go into at this time. Suffice it to say for our present purposes, it has become increasingly important to learn more about the functions of the different commissures and also about the physiological properties of commissurotomized brains in their various forms, not only for the direct information obtained, but also with regard to the application of these preparations to other problems.

Although the old riddle of the corpus callosum, as such, has been largely resolved in recent years, the great cerebral commissure still presents something of a riddle with respect to the meaning of the prevailing symmetry of its fiber connections. Anatomical and physiological studies indicate that the majority of the callosal fibers tend to interconnect corresponding points in the two hemispheres (Bremer, Bridhaye, & Andre-Balisaux, 1956). More than that, it is suggested (Grafstein, 1959) that the fiber systems, arising from different layers within a given locus, tend to connect symmetrically with corresponding layers in the same locus on the opposite side.

What is accomplished by having this huge system of symmetrical cross connections in the highest control centers remains a puzzle. For example, what would be served by having the incoming information from one-half of the visual field interact symmetrically with that of the other half field? At first glance, the effect would seem to be about as helpful as a double exposure in photography. The same may be said for symmetrical cross-interaction of cutaneous information in stereognosis.

The simple principle of homotopic cross connection is illustrated on the left in Figure 3, for comparison with an alternative principle of possible interconnection on the right that I once favored, before the evidence for symmetrical, or homotopic, projection had become so strongly established. It may still be possible, despite the trend of the evidence, that something of the sort depicted on the right is really involved, i.e., that the callosum is not mainly or primarily so much a symmetrizing influence, as it is a means of supplementing the activity of each hemisphere with different and complementary information about what is happening on the other side. It appears there is something special and nonsymmetrical about the cross connections between the





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in the cross-integration. However, it looks as if more is happening in some of these situations than a mere leakage of the sensory data. Possibly such cross-interactions are achieved by devious lower level devices that don't violate the notion of separate right and left mental systems. However, in view of evidence like the foregoing, it seems advisable to keep in mind the possibility that some of our earlier notions regarding the gnostic independence in the separated hemispheres may have to be qualified, as we learn more about the extent and nature of the potentialities for interhemispheric integration at lower levels.

and Myers (1960) in the monkey, its occurrence has been more intensively investigated and confirmed in the last few years by Glickstein (1960a; 1960b). The callosum was clearly playing an important transfer role when present, but even slight leakage of learning effects, across the mid-line following commissurotomy, had become critical with respect to certain uses of the split-brain preparation. That either forelimb can be governed from a single hemisphere, in both learned and unlearned activities in the split-brain cat and monkey, seems well established (Schrier & Sperry, 1959; Sperry, 1958; Trevarthen, 1961).

In other tests involving conditional sensory-sensory cross integration between the divided hemispheres (Sperry 1958; 1959), we found that visual information entering on one side can be cross-integrated with tactile information entering the other, even in deep-split cases with section of the midbrain as well as forebrain commissures. It has since been found by Meikle and Sechzer (1960), using cats, and by Trevarthen (1960, 1961), using monkeys, that easy brightness discriminations learned with one eye, transfer to the other in split-brain preparations. According to Trevarthen (1961), color discriminations similarly show some interocular transfer in the split-forebrain monkey. Bisection, through the habenular and posterior commissures and quadrigeminal plate in the monkey, seems to block the transfer of color, but not that for brightness discriminations. Simple visual pattern discriminations may show signs of interference (i.e., transfer effects) in the split-forebrain monkey, when tested by means of simultaneous reversal learning—i.e., under training and testing conditions that favor the detection, rather than occlusion, of the more subtle interactions between the divided hemispheres. Recently it has been shown that a visual brightness discrimination can be performed by split-brain cats (Robinson & Voneida, 1961) and monkeys (Trevarthen, 1961), when one brightness is projected through the left eye and the other through the right. Some of our split-brain monkeys are also performing size discriminations under these conditions as, for example, when one of four open circles of graded sizes is projected to one of the separated hemispheres and a second simultaneously to the other. Thus, cross comparisons for correct judgment of relative size are somehow achieved across the divided hemispheres, the surgical sections in this case extending through the anterior half of the quadrigeminal plate. Conditioned response studies, being carried out with conditioned tactile stimuli (Meikle, 1961) and with conditioned visual stimuli (Voneida and Sperry, 1961) in split-brain cats, are also revealing cross-integration effects.

In most of the above cases, the analysis has not been carried far enough so that one can say what phase of the neural process is involved



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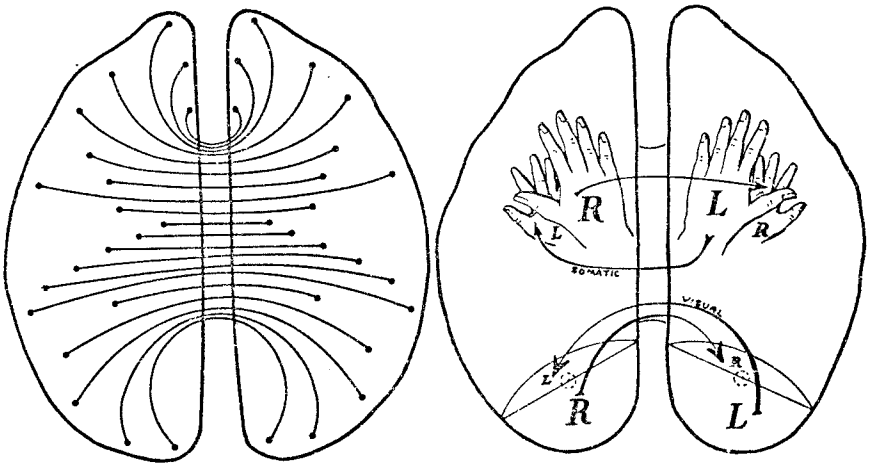


*Fig. 3.* Projection of corpus callosum: Simple homotopic projection principle on left compared with that of speculative "supplemental complementarity" on right.

visual areas (Bremer, Brihaye, & Andre-Balisaux, 1956; Myers, 1960). In the somatic cortex, where contralateral and ipsilateral points tend to be pretty much in register, the two alternatives shown here would be difficult to distinguish from the data now available. The scheme on the right accords better also with the development of lateral dominance in the human brain.

This leads to one more general point that boils down essentially to a note of caution. In earlier studies of interhemispheric transfer after callosum-section, including those of Myers (1956) and others (Sperry, Stamm, & Miner, 1956) on visual discrimination learning in the cat, those of Stamm and myself (1957) on somesthetic learning in the cat, and those on visual learning in the monkey (Downer, 1958; 1959; Sperry, 1958; 1959), it was found regularly that section of the cerebral commissures prevented the spread of learning and memory from one to the other hemisphere. It was as if each of the separated hemispheres had a complete amnesia for the experience of the other, as if each had its own independent perceiving, learning, and memory systems.

Upon extending our transfer studies in the monkey from visual to somesthetic and motor learning (Sperry 1958; 1959), the independence of the separated hemispheres was less clear-cut, in that some of the monkeys on some problems demonstrated rather strong transfer of learning from one to the other hand. Although such transfer was not seen in the later studies by Myers (1960) in the chimpanzee, or by Ebner